1 **Title:** Broader niches revealed by fossil data don't reduce estimates of range loss and
2 fragmentation of African montane trees

3 **Short title:** The future of African montane forests

4 **Keywords:** tropical climate, paleoecology, biogeography, species distribution models, niche,
5 tropical forests, range collapse, Afromontane

6 **Abstract**:

7 *Aim:* Many species' climate tolerances are broader than those estimated from current native

8 ranges. Indeed, some Afromontane trees' niches are up to 50% larger after incorporating fossil

9 data. This expansion could reduce estimates of species' future range loss due to climate change

10 but also implies strong non-climatic limitations on species' current ranges. One such limitation is

11 land use, which fossil data suggest influences Afromontane tree distribution, preventing these

12 trees from occupying warmer conditions than they currently do. We aim to assess the degree to

13 which the broader climatic tolerances revealed by fossil data buffers projected range loss from

14 climate and land use for Afromontane trees.

15 *Location:* Africa

16 *Time period:* Last 21,000 years

17 *Major taxa studied:* Afromontane trees

18 *Methods:* We used species distribution models informed by both current and fossil distributions

19 to project future ranges under climate and land-use projections.

20 *Results:* We found that projected range reductions are only slightly ameliorated by incorporating

21 fossil distributions and these improvements diminish further under severe land use or climate

22 change scenarios. Taxa that are less impacted by climate are more impacted by intense land use.

23 Depending on the severity of climate and land use, the geographic extent of Afromontane tree

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24   species' ranges will contract by 40-85% and the trees will completely be lost from large portions

25   of Africa. We projected that the surviving species' ranges will become increasingly fragmented.

26   *Main conclusions:* Maintaining Afromontane ecosystems will require mitigation of both climate

27   and land-use change and protecting areas to optimize connectivity. Our findings caution that

28   species with climate tolerances broader than their current range might not necessarily fare better

29   under strong changes in climate or land use.

30   **Introduction:**

31   Climate change over the 21st century is expected to contribute to species extinctions and

32   turnover (Petersen et al. 2002; Urban 2015). These risks could be particularly pronounced for

33   montane taxa, as high-elevation species could experience a complete loss of suitable climate

34   conditions on the mountains where they occur (Petersen et al. 2002; Williams et al. 2003). A

35   principal tool for assessing these risks is to construct climatic Species Distribution Models

36   (SDMs), which use the climate conditions species experience within their modern distributions

37   to assess future potential distributions under climate change (Pearce and Ferrier 2000; Guisan

38   and Thuiller 2005; Elith and Leathwick 2009; Urban 2015; Lenoir and Svenning 2015). One

39   limitation of this approach is that the realized niche that organisms presently occupy may

40   represent only part of the climatic conditions they can actually tolerate, and other conditions

41   might also be suitable for species persistence (Araujo and Pearson 2005). Omitting currently

42   unoccupied conditions that are climatically suitable will underestimate species 'climatic niches'

43   and overestimate the risks posed by climate change. However, including these conditions is

44   difficult as the differences between climatic tolerances and distributions are likely to be species-

45   specific and are generally unknown (Sax et al. 2013).

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46   Recent work comparing species' native and non-native populations does suggest that

47   some species' native ranges do not fully reflect their climate tolerances (e.g., Gallagher et al.

48   2010; Early and Sax 2014). In addition to non-native distribution data, there has been a strong

49   call in the literature for increased use of fossil distribution and paleoclimate data to improve

50   measurements of species' climate niches (Botkin et al. 2007; Nogues-Bravo 2009; Veloz et al.

51   2012). Maiorano et al. (2013) showed how realized niches change through time and that

52   "building a niche" with fossil data altered current and future range projections. Nogues-Bravo et

53   al. (2016) showed that the inclusion of fossil data in SDMs more accurately assessed

54   conservation risk for plant genera and families in Europe and North America. Ivory et al. (2016)

55   used fossil data to show that some Afromontane trees previously occupied warmer conditions

56   than in their current distributions. This is supported by paleoecological studies which find that

57   anthropogenic impacts since at least the Iron Age have progressively altered East African

58   species' distributions through changing land use and fire regimes (Hall et al. 2009).

59   Climate change and land use have long been appreciated as a dual threat to species

60   persistence, particularly when anthropogenic activities block species' range shifts (Hansen et al.

61   2001; Feeley and Silman 2010; Barbet-Massin et al. 2012). Some work suggests that future

62   changes in land use might be particularly important to species distributions in the tropics (Jetz et

63   al. 2007). Recent reviews and conceptual considerations of climate and land-use change have

64   concluded that estimates of extinction risk should consider both factors, while acknowledging

65   the challenge of considering dual risks that could interact in complex ways (De Chazal and

66   Rounsevell 2009; Oliver and Morecroft 2014).

67   The Afromontane forest is an excellent example of a system where the interplay between

68   future changes in land use and climate might be particularly important. This region is a globally

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69   unique biodiversity hotspot, characterized by a rich endemic flora, and a distinctive set of tree

70   species with broad geographic distributions (White 1981; Mittermeier 2004; Plumptre et al.

71   2007; Ivory et al. 2016). Afromontane forests occupy mountaintops across Africa, extending

72   across the tropics and two temperate zones - from the southern Cape of South Africa to the

73   Arabian Peninsula and from West Africa to Madagascar. It is becoming clear that even such

74   extensive systems are at risk from climate change and land use in the future; however, the degree

75   to which each will impact species' ranges is currently unknown (Mittermeier, 2004; Niang et al.,

76   2014). Indeed, given current climate conditions and estimated niche requirements, the potential

77   range of certain species, such as *Olea africana*, could be as much as 50% larger than their

78   current realized distributions (Ivory et al. 2016). This expanded tolerance could buffer these

79   species from some extent of future warming. Likewise, Afromontane tree species' extensive

80   distribution and potential capacity to shift their ranges upslope could also buffer them from a

81   warming climate. Alternatively, Afromontane ecosystems might be disproportionately at risk,

82   because Africa is already one of the warmest places on Earth and is predicted to warm more

83   dramatically than other tropical continents by the end of this century (Dullinger et al. 2012;

84   Gottfried et al. 2012; Niang et al. 2014). Likewise, regional human populations are rapidly

85   increasing (Lopez-Carr et al. 2014), suggesting that land use is likely to intensify. The rate of

86   land conversion is predicted to increase in Africa due to rapid population growth and intensified

87   agriculture, reducing available habitat and causing extensive disturbance to natural ecosystems

88   (Feeley and Silman 2010; Niang et al. 2014). If future human land use extends to higher

89   elevations, this could further imperil the Afromontane ecosystem to reduce available habitat.

90   Ultimately, Afromontane forests could provide an excellent system to investigate how species

91   with (i) tolerance to warmer conditions than those currently experienced, (ii) the capacity to

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92   move upslope, and (iii) a broad geographic extent, will fare in response to the dual threats posed

93   by future changes in climate and land use.

94   Here we use SDMs developed by Ivory et al. (2016) using current and fossil occurrences

95   of eight Afromontane tree taxa to evaluate the risks posed from future changes in climate and

96   land use. We examine low and high change scenarios for both climate change and land use to

97   consider the role of these threats both individually and together. We evaluate how the relative

98   importance of each varies with the degree of change. We also evaluate the degree to which

99   information on climate tolerances obtained from fossil data reduce range loss relative to

100   predictions based on climate tolerances calculated solely from modern occurrences. We then ask

101   whether the effect of fossil data on any future range loss predictions attenuates with increasing

102   environmental change. Next, we examine whether the patterns observed can be better understood

103   by considering projections in elevational shifts in distribution and changes in geographic extent

104   of these taxa. Finally, we consider the long-term fate of this unique system.

Materials and Methods

106   Afromontane forest covers an area of 98,685 km^2 throughout tropical and southern

107   Africa, beginning at an elevation of ~1500 m asl (Bussman, 2006). Currently, this region is at

108   great risk due to intensifying land use pressure from deforestation, agricultural expansion, and

109   for use of certain plants as non-timber forest products (Niang et al. 2014). SDMs for the eight

110   focal taxa (*Hagenia abyssinica*, *Ilex mitis*, *Juniperus procera*, *Nuxia* spp., *Olea africana*, *Olea*

111   *capensis*, *Podocarpus* spp., *Prunus africana*) were developed by Ivory et al. (2016) and the

112   methods used are discussed extensively in that manuscript. Vegetation zones vary slightly from

113   mountain to mountain and also by aspect but generally have montane forest or rainforest until

114   ~2700 m asl, a zone of bamboo until ~3000 m asl, and are topped by an Ericaceous forest or

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115 cloud forest until the treeline near 3900 m asl (Hedberg 1951; White 1981; Bussman 2006).

116 *Nuxia spp* (Stilbaceae), *Ilex mitis* (Aquifoliaceae)*, Olea africana* (Oleaceae), and *Olea capensis*

117 (Oleaceae) often are found in the mid-altitudes from 1500-2700m asl on wetter slopes (White

118 1981; Bussman 2006). *Prunus africana* (Rosaceae) is an endemic tree that can be found in

119 Afromontane rainforest habitats from 1500-2300m asl m asl (Bussman 2006). *Podocarpus* spp.

120 (Podocarpaceae) are the most characteristic tree of the region, and therefore different species can

121 be found in association with other trees or in monodominant stands at many elevations >1500 m

122 asl (White 1981). *Hagenia abyssinica* (Rosaceae) is a characteristic endemic tree occurring

123 between 2900-3300 m asl and is a commonly used medicinal plant (Bussman 2006; Assefa et al.

124 2010). Above this zone and up to the treeline at 3500-3900 m asl, Ericaceous forests commonly

125 include *Juniperus procera* (Cupressaceae).

126   Species occurrence records were acquired from two sources. Observations of modern

127 species occurrences were retrieved from the Global Biodiversity Information Facility (GBIF;

128 www.gbif.org). Modern occurrences were supplemented by modern pollen datasets, which were

129 taken from the African Pollen Database (APD; http://fpd.sedoo.fr/fpd/; Vincens et al. 2007b).

130 Fossil pollen samples were also acquired from the APD and taken from two data-rich periods in

131 the paleoecological record, which were used in Ivory et al. (2016): the mid-Holocene (MH;

132 6ka), and Last Glacial Maximum (LGM; 21ka). The taxonomic resolution of all pollen taxa

133 matches the stated descriptions above with six determined to species level and the remaining two

134 to the genus level (*Nuxia* spp. and *Podocarpus* spp.). All pollen data were converted to relative

135 abundances, then presence or absence of the taxa was determined based on the method

136 developed by Ivory et al. (2016). This method used studies of pollen transport to set a threshold

137 value of abundance that indicates the taxon presence within each climatic grid-cell. Four

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138 climatic variables (gridded at 10' resolution) were extracted from Worldclim

139 (www.worldclim.org) to estimate modern and past distributions (mean annual temperature

140 [MAT], mean annual precipitation [MAP], diurnal temperature range [Diurn], and rainfall

141 seasonality [Seas; coefficient of variation]). The gridded modern climate data was compared to

142 weather station data and found to accurately capture gradients in temperature and precipitation

143 (Hijmans et al. 2005; Ivory et al. 2016).

144   For this study, future potential ranges were forecasted using climate model output for the

145 end of the century (2061-2080), which were downscaled to 10' resolution as part of the

146 Worldclim climate dataset (Fig. S1; Hijmans et al. 2005) and projected using a Lambert

147 Azimuthal equal-area projection for analyses. Higher resolution climate data were not used as

148 Africa has relatively few weather stations that can be used to spatially downscale climate data

149 and such data, if used, would have had values with considerable uncertainty (Hijmans et al.

150 2005). Future climate conditions were predicted using an ensemble of output from the most

151 recent Climate Model Intercomparison Project (CMIP5), integrating output from five climate

152 models: NCAR CCSM4 (Gent et al. 2011), HadGEM2-ES (Collins et al. 2011), MIROC-ESM

153 (Watanabe et al. 2011), IPSL-CM5A-LR (Dufresne et al. 2013), and NorESM1-M (Bentsen et al.

154 2013). We used Representative Concentration Pathways (RCPs) 2.6 and 8.5 to forecast future

155 ranges to evaluate the magnitude of climate change on ranges for each taxon (Fig. S1). In 2061-

156 2080, average MAT at occurrence locations will be 1.4°C + /-0.7°C warmer under RCP 2.6 and

157 3.4°C + /-1.1C warmer under RCP 8.5 (Table S1). All principal analyses in the manuscript use

158 the ensemble model (Table S1). However, we also ran a secondary set of analyses using just

159 output from HadGEM2, which predicts the largest increase in MAT (+4.6°C) and provides a

160 "worst case scenario" for climate change. Further, to evaluate the impact of extrapolation to no-

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161 analogue climate conditions in the future for our taxa of interest, we used the MESS package in

162 R to illustrate that climate forecast under RCP 8.5 has analogous climate in the Afromontane

163 region today, avoiding extrapolation (Elith et al., 2010; Fig. S7).

164   To project each taxon's future potential range, SDMs were constructed using all

165 regression and machine learning algorithms in BIOMOD2 using R (Thuiller et al. 2009; R Core

166 Team 2017). We used an area under the receiver operating curve [AUC] threshold of >0.80 to

167 define the best performing models and constructed a total consensus ensemble of these models.

168 AUC, a common SDM assessment tool, is a metric of the true number of presences as a function

169 of the number of false positives. These values are presented in the Appendix (Table S5), and

170 there is no significant difference between AUC values based on modern-only versus modern and

171 paleoecological occurrences (t = -0.803, p = 0.4356). Previous studies have illustrated the

172 application of ensemble forecasts in relation to individual models (Araújo and New 2007). To

173 compare the influence of including paleoecological data in future range projections, we created

174 two sets of SDM ensembles for each taxon: (1) SDMs trained on the modern-only occurrences,

175 and (2) SDMs trained on the modern and paleoecological occurrences combined. Due to the lack

176 of information about species' true absences, pseudo-absences (eight times the number of

177 occurrences) were randomly selected from a 400 km radius around occurrences. This follows

178 commonly used methods, such as VanderWal et al. (2009), who found that this distance balanced

179 over-fitting SDMs to local distributions versus not including radically different climates in the

180 models. K-fold cross validation was performed for model validation in which the occurrences

181 were randomly split into training and testing datasets (70% and 30% split) three separate times.

182 The final models for the modern-only or modern + paleoecological datasets were constructed

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183   using 100% of the occurrences. A threshold to designate presence versus absence of a species

184   was calculated based on the True Skill Statistic (TSS) for each model.

185   We use gridded projections of land-cover change from the Integrated Assessment Models

186   (IAMs; Moss et al. 2010) for the end of the century (2061-2080) to represent the potential impact

187   of future land use. IAMs are a tool for integrating disparate information from different

188   disciplines (i.e. physical, economic, and social processes), which can help scientists and

189   decision-makers understand the outcomes of complex environmental problems like

190   anthropogenic change. To do this, we considered two end-members representing high and low

191   intensity land-use scenarios: the Model for Energy Supply Strategy Alternatives and their

192   General Environmental Impact (MESSAGE) and the Integrated Model to Assess the Global

193   Environment (IMAGE), respectively (Moss et al. 2010). We will refer to the MESSAGE

194   scenario as "high land use" and IMAGE scenario as "low land use". SDM projections of tree

195   ranges were compared to projections of land use to evaluate the impact of land-use change, and

196   grid-cells projected to be unsuitable for natural vegetation were eliminated from SDM forecasted

197   ranges for each individual taxon. We considered a grid-cell as unsuitable for natural vegetation

198   when the summed area of agricultural land, pasture land, and urban areas covered >90% of the

199   grid-cell (Fig. S2 and S3).

200   After forecasting potential ranges for each taxon under future climate, we employed the

201   PatchStats package in R (McGarigal and Cushman 2002) to estimate fragmentation of forest

202   populations. This package allowed us to calculate the mean size, number, and connectivity of the

203   patches (contiguous grid cells) for each taxon across the forecasted ranges for each combination

204   of climate and land use.

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205   We performed a series of sensitivity tests to evaluate how the ranges of Afromontane tree

206   taxa will respond to individual environmental variables at different elevations. For these tests, we

207   projected future ranges using future values of one climate variable, but retained modern values of

208   all other variables. We repeated this for all climate variables. The range sizes that resulted from

209   these projections were then compared to those from projections using future values of all climate

210   variables, presented in Figure 1. This allowed us to calculate the proportion of range change at

211   the end of the century that resulted from each climate variable (1 = contributed to range

212   expansion; -1 = contributed to range contraction). We parsed these results for each taxon into

213   200m elevational bands (between 1200-3800 m asl) to estimate the impact on range sizes of

214   projected future change in each climate variable individually.

215   **Results**

216   *Geographic Range Contraction*

217   We forecast that by the end of the 21st century all Afromontane taxa could experience a

218   range-size reduction under all combinations of climate and land-use change (Fig. 1 and S4; Table

219   1). However, based on the SDMs constructed from modern and fossil occurrences for our eight

220   focal taxa, range contraction is projected to vary considerably depending on the combination of

221   climate and land-use change. We illustrate this variation by showing range loss associated with

222   the individual and combined effects of RCP 2.6 (moderate climate change; +1.4°C), RCP 8.5

223   (large climate change; +3.4°C), a low land-use scenario, and a high land-use scenario for two

224   exemplar taxa (Fig. 1) and for the remaining six taxa (Table 1; Fig. S4). The average range loss

225   impacts of RCP 2.6 are more severe than those from a low land-use scenario alone; likewise, the

226   average impacts of RCP 8.5 are more severe than those from a high land-use scenario alone

227   (Figs. 1 and 2). However, among taxa there is considerable variation. Some taxa, such as *Olea*

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228   *africana*, show a similar magnitude of range loss from both climate and land-use scenarios (Fig.

229   1; Table 1). In contrast, other taxa, such as *Prunus africana*, show a very high magnitude of

230   range loss from climate but very little impact from even intense land use (Fig. 1; Table 1). On

231   average across all taxa, the impacts of even a small change in climate are more severe than those

232   of high intensity land use (Fig. 2; Table 1). Not surprisingly, the strongest impacts on range loss

233   are observed when RCP 8.5 and a high intensity land-use scenario are combined (Fig. 1, 2, and

234   S4), which results in an average range reduction of 79% (Table 1). Considering the impact on

235   this group of taxa as a whole, the extent of area where all representative taxa are lost increases

236   with increasing scenario severity (Fig. 3). The combination of these dual impacts results for

237   many individual taxa in the complete extirpation from certain regions (Fig. 1, Fig. S4). Under

238   high land-use and RCP8.5, all studied taxa are lost from Madagascar, tropical western Africa,

239   most of the Arabian Peninsula, and much of southern Africa (Fig. 3).

240   Future range forecasts based on both modern and fossil occurrence data on average decrease

241   range loss only slightly relative to range loses calculated using solely modern occurrences (Table

242   1). For example, the average amelioration in range loss among taxa for RCP 2.6 with and

243   without fossil occurrences is only 7% (Fig. 2). Some taxa, particularly those which Ivory et al.

244   (2016) demonstrated to have occupied warmer climates in the past, show a moderate decrease in

245   range loss. These taxa, *Olea africana*, *Olea capensis*, and *Podocarpus* spp., together average

246   15% lower range loss when fossil data are included (Table 1). Most importantly, the magnitude

247   of the ameliorating effect attenuates with increasing severity of land use and climate change (Fig.

248   2). The average amelioration in range loss with and without the fossil data for RCP 8.5 is only

249   2%, and this difference is only 9% for the three taxa highlighted above.

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250   In addition to the results described above, we predicted range changes based on the

251   HadGEM2 model output, which forecasts more extreme warming (+4.6°C) than the CMIP5

252   ensemble. The results are similar, but slightly more severe (Fig. S5; Table S2). For example, the

253   potential ranges for all taxa decrease more strongly under RCP 8.5 from HadGEM2 than under

254   the CMIP5 ensemble forecast (5% more range loss on average; Table S2). Further, the forecast

255   range reduction from the combined effects of RCP 8.5 and the high land-use are on average 2%

256   greater under HadGEM2 than those forecast based on the ensemble model (Tables 1 and S2).

257   *Elevational Range Contraction*

258   Future range forecasts using both modern and fossil data predict that the total area occupied

259   at individual elevation bands will be greatly reduced by the end of the century. We illustrate this

260   with two exemplar species (Fig. 4), together with the remaining six taxa (Fig. S6). There is much

261   variation in the change in geographic extent among taxa. Some taxa, e.g., *Olea africana*, lose

262   relatively little suitable habitat under RCP 2.6 (Fig. 4), and most lose relatively little suitable

263   habitat under the low land-use scenario (Fig. S6). Total reductions in elevational range under

264   RCP 8.5 are universally high (Fig. 4, Fig. S6). Importantly, the ranges of all taxa, except for *Olea*

265   *africana*, are forecast to contract at lower elevations without a concomitant upward expansion

266   (Fig. 4, S6). Sensitivity analysis of the climate variables used for the SDM range forecasts shows

267   that most lower-elevation range loss is driven by temperature (Fig. 4; Fig. S6). Future

268   temperature increases result in a particularly notable impact at middle elevations (between 2000-

269   2800 m asl); however, projected changes in diurnal temperature and rainfall buffer against

270   reductions in climatic suitability in these elevations (Fig. 4; Fig. S6).

271   *Habitat Fragmentation*

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272   Our SDM range forecasts based on modern and fossil occurrences show marked reductions

273 in patch size, number, and connectivity. This results in fewer, smaller, more isolated patches as

274 climate and land-use change intensifies (Fig. 5). Patches of all sizes become less frequent, the

275 largest patches become fragmented, and ~30-50% of the smallest patches disappear (<5000 km^2;

276 Fig. S2). Forecasts based solely on RCP 8.5 result in greater reductions in patch size and number

277 than forecasts based on high land use and RCP 2.6. In contrast, patch connectivity is reduced

278 more by high land use together with RCP 2.6 than by RCP 8.5 alone (Fig. 5).

279 **Discussion**

280   Across the Afromontane region, future climate and land-use change could result in large-

281 scale collapse of this widespread montane ecosystem. Using paleoecological data, Ivory et al.

282 (2016) found that Afromontane trees could tolerate warmer climates than they currently occupy,

283 suggesting that they could be less threatened by climate change than one might expect. We show

284 here that although including fossil distribution data does decrease forecasted range loss, the

285 amelioration is small and diminishes in importance with increasing severity of climate change.

286 The difference between range loss predicted with and without fossil data becomes almost

287 negligible under RCP8.5 (Fig. 2).

288   Our findings contrast with other studies, such as Nogues-Bravo et al. (2016), which found

289 a strong reduction of range loss when including fossil data for projecting future conservation

290 risks for plants in North America and Europe. Such qualitatively different responses to

291 incorporating fossil data could have many explanations. The results of Nogues-Bravo et al.

292 (2016) might have been influenced by their grouping of species into genera and families,

293 whereas we studied responses at the species level for 6 of our 8 plant taxa. Alternatively, these

294 differences might also be due to inherent differences of temperate and tropical species. The

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295　thermal niches of tropical species are expected to be narrower than temperate species and to

296　show greater conservatism through time. Finally, it is also possible that differences in species

297　diversity and competitive interactions within the tropics may influence this result.

298　　　The relatively minor impact of including information about the types of climates

299　occupied in the past on the niches in our study might be due to the specific effects of climate

300　change in tropical highlands. It is clear from studies of past vegetation (Dupont et al., 2011;

301　Ivory et al., 2018) and previous SDM work (Ivory et al., 2016) that some Afromontane taxa

302　formed continuous forest corridors in the lowlands during past warm periods. Further, in the

303　tropics, changes in rainfall and seasonality are known to have played a strong role in range

304　changes in the past (Vincens et al., 2007a). We demonstrate that this is also likely true in the

305　future, as projected changes in other climate variables, like diurnal temperature and rainfall,

306　buffer against range loss reductions for many taxa at certain elevations. This suggests more

307　complex responses to climate change than would be expected from temperature alone.

308　　　Our findings suggest that the magnitude of climate change forecasted under RCP 2.6 is

309　actually quite large for Afromontane taxa, leading to range loss of up to 42% for certain species,

310　even with niche requirements estimated from modern and fossil occurrences. Africa is expected

311　to warm more than other tropical continents (Niang et al. 2014). This means that even ambitious

312　greenhouse gas reduction targets result in relatively large increases in mean annual temperature

313　(+1.4°C; Table S1) and plant distributions.

314　　　These results also differ from work on other regions, such as South America and Europe,

315　where species have shown range contraction at lower elevations and expansion upslope in

316　response to climate warming (Feeley and Silman 2010; Dullinger et al. 2012; Gottfried et al.

317　2012; Duque et al. 2015). In contrast, these Afromontane taxa are not forecast to expand

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318   upslope. This likely results from an important physiographic attribute of this system: that African

319   mountaintops are generally spatially quite small and discontinuous. Thus, currently there is very

320   little area at higher elevations that is not already occupied by these taxa (Fig. 4; S6). In fact,

321   Afromontane trees already occupy over 90% of available land area at these elevations, leaving

322   little available for future upslope expansion (Fig. 4; Elsen and Tingley 2015). These species also

323   are not forecasted to expand to cooler climates northward or southward, as they already occupy

324   most mountains on the African continent. We therefore suggest that a lack of suitable upslope

325   habitat drastically reduces the capacity of these taxa to adapt to changing climate.

326   Although the impacts of land-use change alone are smaller than the impacts of climate

327   alone, the combined effects of climate and land-use change can be extremely large (Figs. 1, 2;

328   Table 1). Range reductions can be as much as 26% larger on average when land use is included

329   than from climate alone when RCP 2.6 is used (Table 1). In fact, the impact of RCP 2.6 plus

330   high intensity land use results in nearly the same magnitude of range loss as for RCP 8.5 climate

331   alone (Fig. 2; Table 1). This suggests that even though climate has the strongest single effect on

332   range reduction, intensifying land use will have a powerful secondary effect. Moreover, some

333   species, particularly those shown by Ivory et al. (2016) to be least sensitive to temperature, are

334   disproportionately affected by land-use change. Incorporating both climate change and land use

335   impacts, *Olea africana* could lose almost half its climatically suitable range from land-use

336   change, as its present, low-elevation range is where future land-use changes are forecast to be

337   largest (Figs. 1 and 4). Thus, even if species can adapt to a changing climate, range loss at the

338   lower range boundary is still likely due to lowland exclusion through anthropogenic activity.

339   Although the high and low intensity land-use scenarios used here can help give us an

340   understanding of the differential impacts of rapidly growing populations in Africa, the indefinite

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341   outcomes of these complex systems injects considerable uncertainty into end-of-century land-use

342   predictions (Pontius and Spencer, 2005). Further, in Africa small-scale land-use changes have

343   impacts beyond those captured in the IAMs, like harvesting of non-timber forest products (e.g.

344   medicines from *Prunus africana* and *Hagenia abyssinica* [Stewart, 2003; Cunningham et al.,

345   2016]). This suggests that the IAMs are likely to be conservative estimates of land-use impacts.

346   Further, many studies investigating the ongoing effects of deforestation in parts of the

347   Afromontane regions suggest massive losses over the last 60 years (Hall et al., 2009) and that

348   land use alone unchecked may result in near total loss of forest (Ngigi and Tateishi, 2004). This

349   is particularly likely given that some of Africa's highlands are already the most densely human

350   populated lands on the continent with populations projected to increase faster than anywhere else

351   on Earth (Plumptre et al., 2004; Linard et al., 2012).

352   The collapse in range size we predict is coupled with forecast changes in the patch size,

353   number, and connectivity of populations across the region (Fig. 5). Habitat connectivity is

354   critical to maintaining viable populations (Shoemaker et al. 2013). In this region, one way this

355   occurs is by maintaining genetic diversity. In Afromontane regions many tree species are

356   dispersed by animals, such as birds, so geographic barriers and the effects of fragmentation may

357   be overcome by long-distance dispersal (White, 1981; Mairal et al., 2017). However,

358   fragmentation leading to small disconnected patches by climate and land-use change result in

359   enhanced edge effects which may lead to regional functional extinctions, or extinction debt

360   (population reduction leading to inevitable extinction) long before species completely disappear

361   (Jackson and Sax 2010; Platts et al. 2013; Haddad et al., 2015). While the quantitative changes

362   we describe here for habitat fragmentation depend on the thresholds used to define land use, the

363   qualitative results themselves are not. For example, we considered a grid-cell as unsuitable for

16

364   Afromontane forest when the summed area of agricultural land, pasture-land, and urban areas

365   covered >90% of the grid-cell. This threshold was chosen as it represented the largest change in

366   land-use distributions with respect to modern within the Afromontane region (Fig. S3). However,

367   many of the taxa considered here occur within grid cells projected to undergo complete land

368   cover conversion, meaning 100% of land area within a grid cell will exclude natural vegetation

369   (Fig. S3). This suggests that regardless of which threshold is chosen as a cutoff for our estimates

370   of grid-cell suitability, anthropogenic activities will have a strong impact.

371   We did not explicitly consider the role of elevated CO_2 or fire in driving the future

372   distributions of Afromontane taxa. However, by incorporating fossil-informed niches into our

373   models from ancient periods with lower than modern CO_2 (~180ppm; LGM) and pre-industrial

374   CO_2 (~280ppm; MH), we have some reference on the potential influence that CO_2 may have.

375   Lower atmospheric CO_2 has been cited a driver of tree decline through enhanced water stress in

376   favor of C4 dominated grasslands with higher water-use efficiency (Bragg et al., 2013).

377   Interestingly, we find that during periods with lower CO_2 than today, Afromontane forest species

378   occurred in warmer areas (Ivory et al., 2016). Given the heterogeneity of regional climate

379   change in comparison to CO_2, we suggest that elevated CO_2 will not be a primary driver of

380   vegetation responses to local climate conditions, but could modulate responses. Fire is also likely

381   to impact species' distributions. Ivory et al. (2018) suggest that the exclusion of highland taxa

382   from the lowlands may for some species be related to fire intolerance. Their observation of

383   increased fire activity in lowland East Africa after 80ka may also play an important non-climatic

384   role in constraining these ranges.

385   Afromontane forests are ecologically important hotspots of biodiversity, not just for plants,

386   but also for endemic birds, mountain gorillas, and other fauna (White 1981; Dulle et al. 2016).

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387   Yet future climate and land-use change could result in large-scale collapse of this now

388   widespread ecosystem. We show that including datasets of fossil distributions can alter range

389   forecasts by counteracting the effect of climate disequilibrium of modern species' ranges, but

390   only by a very moderate amount for Afromontane taxa. We show that these taxa will lose a

391   minimum of ~65% of their modern range under high emission and low land-use scenarios (Table

392   1). Even with large emissions reductions (RCP 2.6), if land-use change is high, more than half of

393   Afromontane tree taxa modern ranges may be lost. Under higher emissions and land use, much

394   of the geographic footprint of this system (~80%) may be entirely lost.

395   In the face of such widespread geographical collapse, it becomes imperative to safeguard

396   patches that will remain. Management strategies that focus on conserving species *in situ* are

397   unlikely to yield favorable results from many areas at lower elevations in a warming climate,

398   even if we were to achieve the RCP 2.6 trajectory. Further, given that RCP 2.6 is unlikely based

399   on existing emissions, and that few low-elevation regions are forecast to be suitable under higher

400   emissions, management efforts should focus on protecting areas at mid- and upper elevations and

401   across elevational gradients. Likewise, conservation efforts should prioritize protecting habitat

402   patches forecast to remain largest such as is in southern Africa, as these will minimize potential

403   extinction debts, and to prioritize areas that can provide critical linkages in maintaining

404   connectivity. Ultimately, our study indicates that fossil data used to expand the known niche

405   requirements of extant tropical species may do little to reduce forecasted threats from climate

406   change or land use, particularly when there are strong non-climatic constraints on potential shifts

407   in species distributions.

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636 **Data Accessibility Statement:** The data supporting the results already exists and is freely
637 available in the Global Biodiversity Information Facility (GBIF) and the African Pollen Database
638 (APD).

639

640 **Tables**

641 **Table 1.** Proportion of the modern range of eight Afromontane taxa forecast to be lost under
642 future climate change and land-use scenarios. Species distribution models used to generate these
643 forecasts were created using both paleoecological (Paleo) and modern occurrences (NO Paleo)
644 and an ensemble of climate models.

|	Climate Only		LU-Only		LU and Climate	
RCP 2.6	Paleo	NO Paleo	LU Low	LU High	LU Low	LU High
Hagenia abyssinica	0.336	0.348	0.152	0.361	0.489	0.645
Ilex mitis	0.421	0.421	0.081	0.272	0.468	0.610
Juniperus procera	0.387	0.387	0.138	0.337	0.514	0.664
Nuxia spp.	0.361	0.427	0.122	0.315	0.483	0.623
Olea africana	0.156	0.287	0.135	0.472	0.302	0.564
Olea capensis	0.190	0.380	0.060	0.201	0.368	0.475
Podocarpus spp.	0.239	0.366	0.063	0.221	0.309	0.453
Prunus africana	0.364	0.400	0.073	0.208	0.431	0.536
Average	0.307	0.377	0.103	0.298	0.421	0.571
	Climate Only		**LU-Only**		**LU and Climate**	
RCP 8.5	Paleo	NO Paleo	LU Low	LU High	LU Low	LU High
Hagenia abyssinica	0.696	0.705	0.152	0.361	0.766	0.857
Ilex mitis	0.732	0.732	0.081	0.272	0.749	0.812
Juniperus procera	0.664	0.664	0.138	0.337	0.746	0.835
Nuxia spp.	0.684	0.714	0.122	0.315	0.736	0.813
Olea africana	0.437	0.584	0.135	0.472	0.588	0.748
Olea capensis	0.602	0.670	0.060	0.201	0.673	0.732
Podocarpus spp.	0.646	0.719	0.063	0.221	0.664	0.741
Prunus africana	0.701	0.720	0.073	0.208	0.730	0.783
Average	0.645	0.689	0.103	0.298	0.706	0.790

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664 **Figures**

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665 **Figure 1.** Future range forecast (2061-2080) of *Prunus africana* and *Olea africana* from species
666 distribution models including fossil and modern occurrence data and using Representative
667 Concentration Pathways (RCPs) 2.6 and 8.5 as well as land-use projections of high and low land-
668 use scenarios (MESSAGE and IMAGE). Range forecasts for the six remaining taxa are shown
669 in Fig. S1. Forecast range retained is shown in black and forecast loss is shown in red (and this
670 percentage of modern range lost is provided as a number below each panel).

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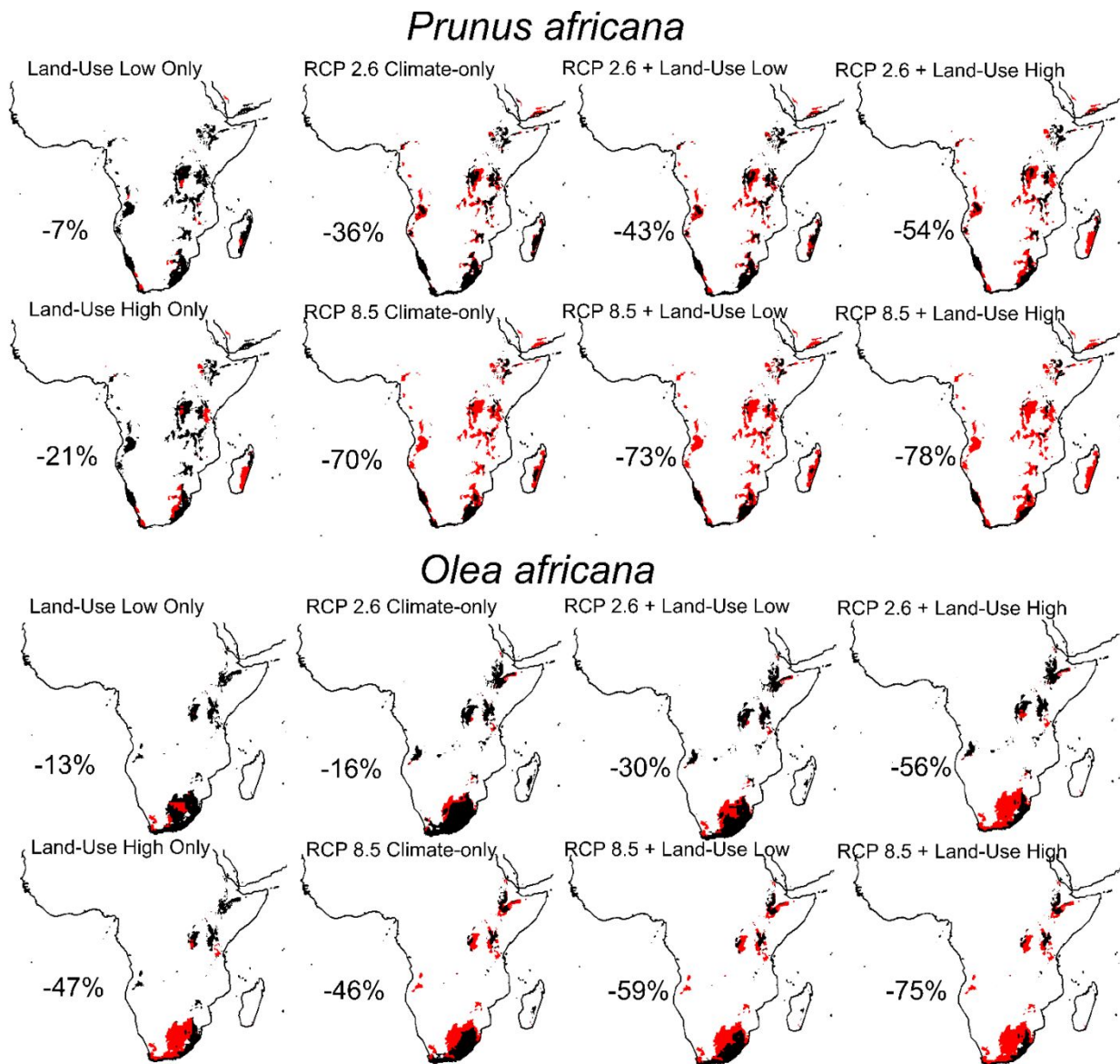
672 **Figure 2.** Range loss for climate and land-use change combinations forecasted to occur on
673 average across species for the end of the century (2061-2080) when SDMs are based on both
674 modern and fossil occurrences (red) or just on modern occurrences (in which case the additional
675 forecasted loss is shown in black).

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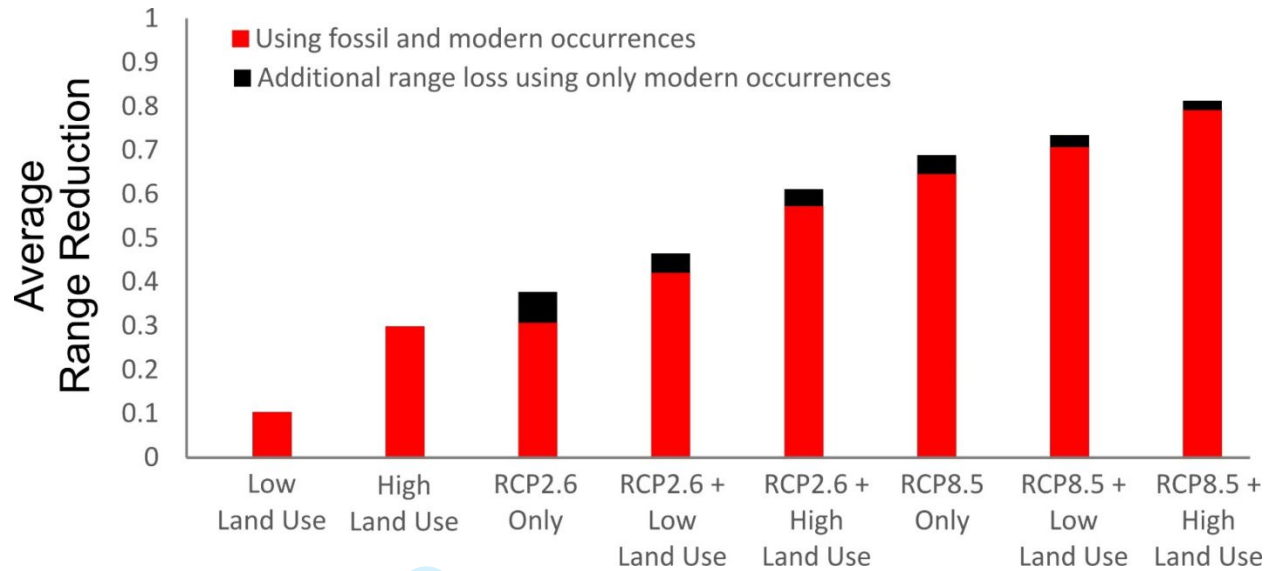
Figure 3. Future range forecast (2061-2080) of all studied Afromontane trees from species distribution models including fossil and modern occurrence data and using Representative Concentration Pathways (RCPs) 2.6 and 8.5 as well as land-use projections of high and low land-use scenarios (MESSAGE and IMAGE). Number of species with forecasted ranges retained are shown and where all forecasted range is lost is in red.


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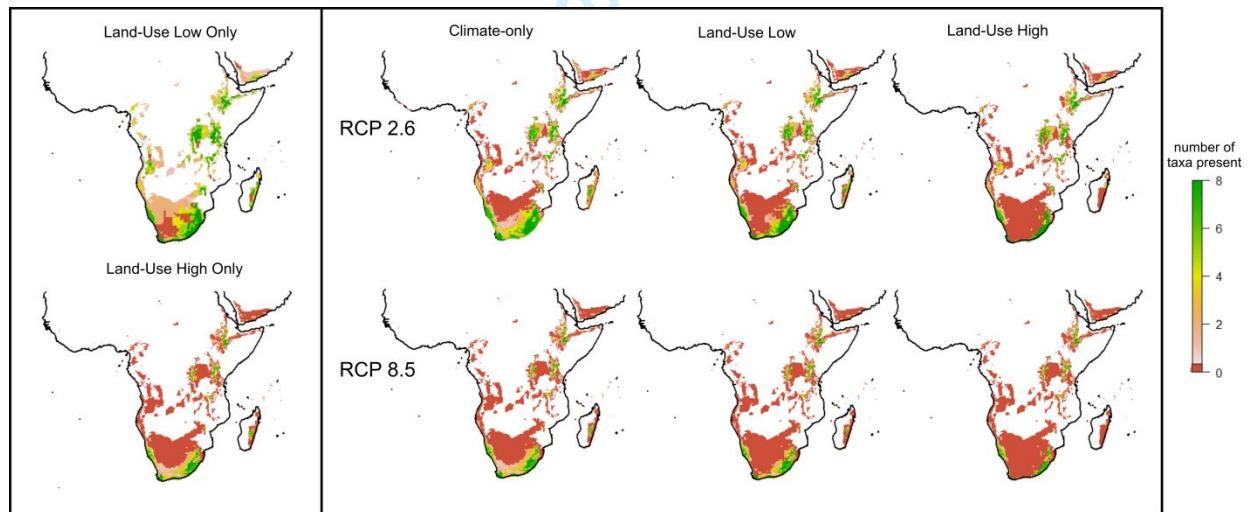
Figure 4. Future range forecast (2061-2080) of *Prunus africana* and *Olea africana* by elevation band from species distribution models including fossil and modern occurrence data and using Representative Concentration Pathways (RCPs) 2.6 and 8.5 as well as land-use projections of high and low land-use scenarios (MESSAGE and IMAGE). Forecasted loss is shown in red and future range in black. Light grey represents the total area available in the elevational band. The right-most panel for each RCP shows the range sensitivity to each climate variable in each elevational band, MAT (mean annual temperature, red), MAP (mean annual precipitation, dark blue), Diurn (diurnal temperature, orange), Seas (rainfall seasonality, light blue). Negative values indicate that a variable contributes to a range contraction, positive values indicate that a variable

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692 contributes to a range expansion. The remaining six taxa elevational range forecasts are shown in
693 Fig. S3.
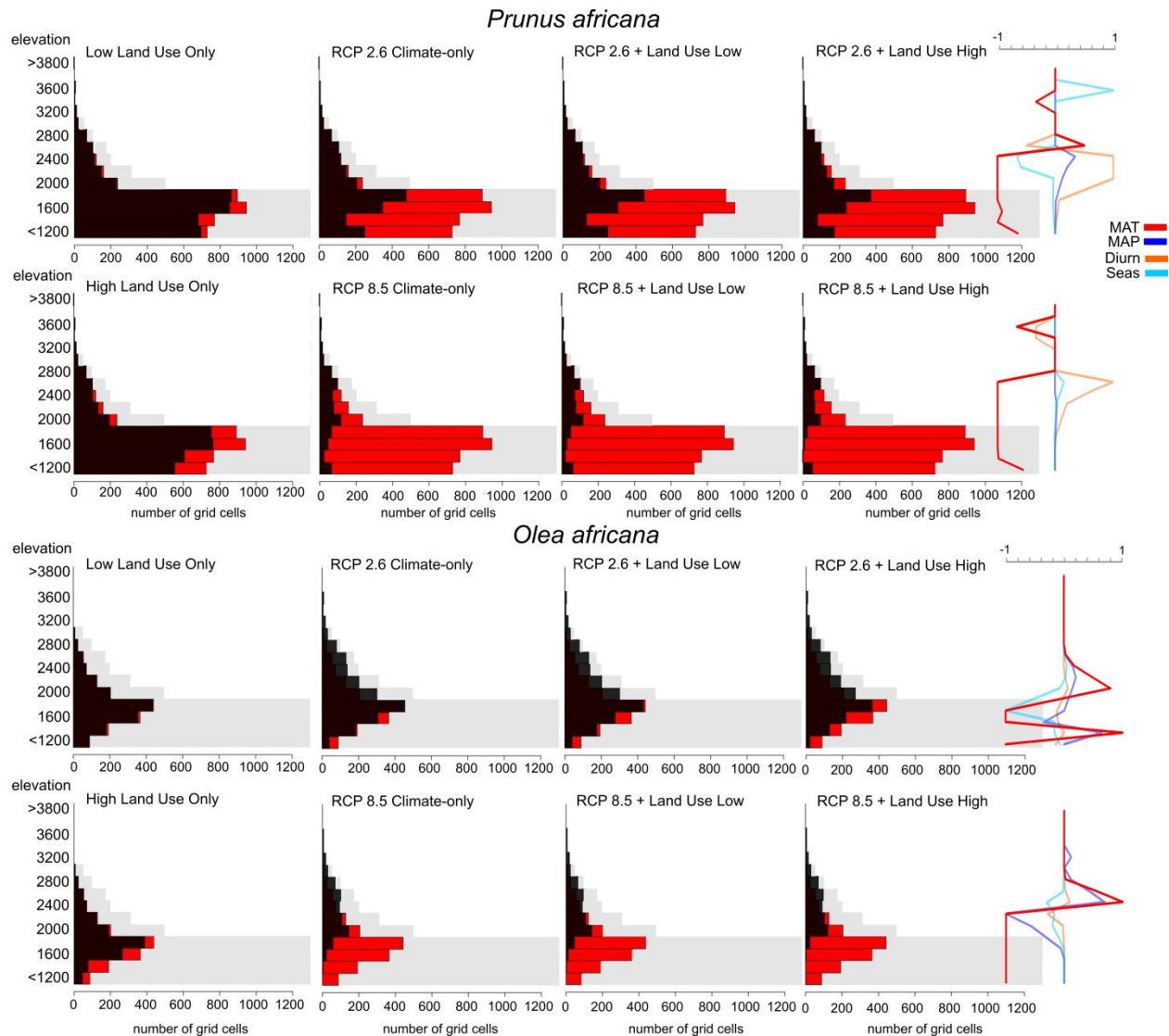
Figure 5. Patch statistics for forecasted ranges of taxa presented in Figures 1 and Fig. S1,
derived using species distribution models including fossil and modern occurrence data and using
Representative Concentration Pathways (RCPs) 2.6 and 8.5 as well as land-use projections of
high and low land-use scenarios (MESSAGE and IMAGE). Mean patch size is the average of
the area of all patches, patch number is the remaining total number of patches, and patch
connectivity is a dimensionless index of patch aggregation on the landscape.

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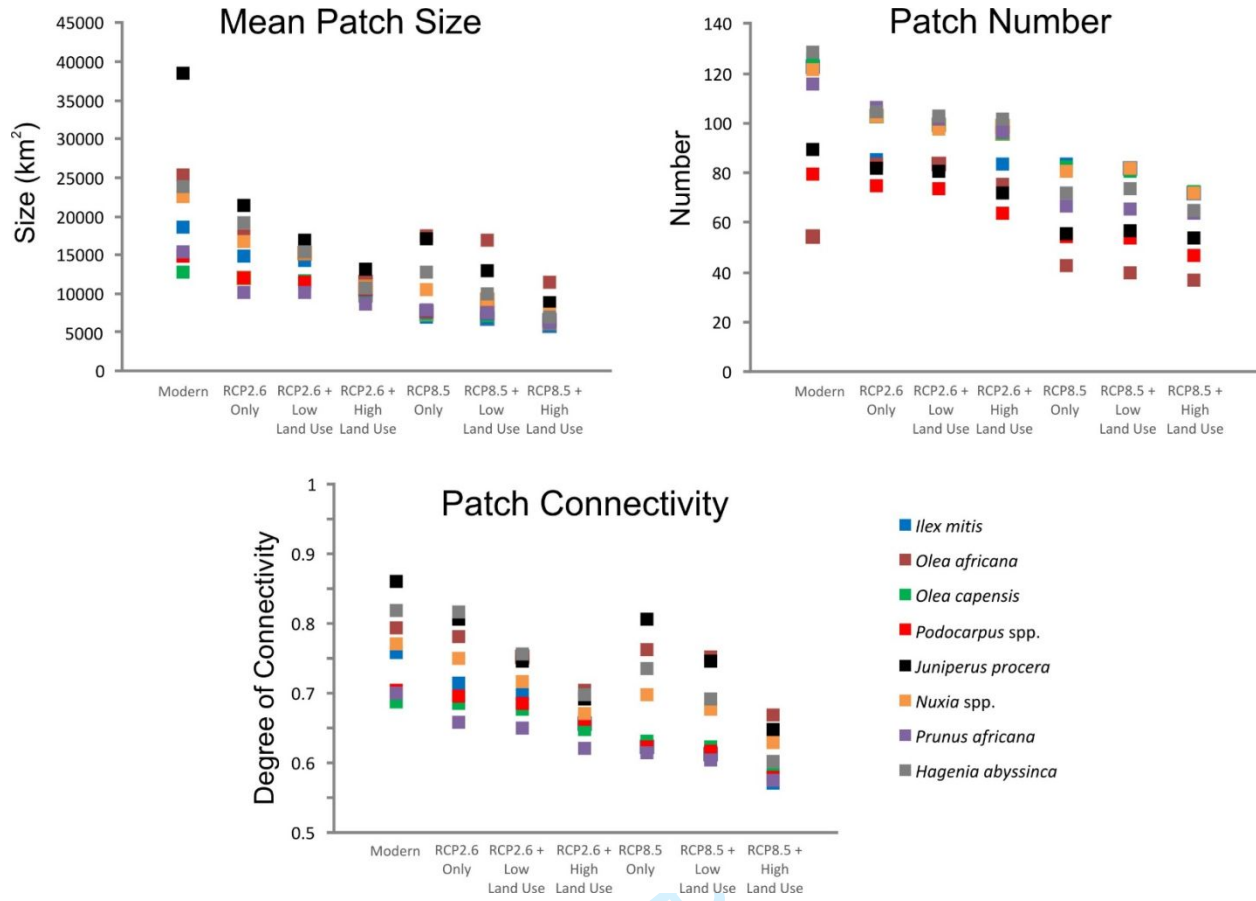
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